# Assessing Biochemical Fitness of Predator *Podisus maculiventris* (Heteroptera: Pentatomidae) in Relation to Food Quality: Effects of Five Species of Prey

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**ABSTRACT** Preferences of female predators for various species of prey may not correlate with nutritional value of the prey, notably with regard to resulting rates of reproduction in the female predator. This study assessed the biochemical status of adult female *Podisus maculiventris* (Say) as affected by prey species. Colony-reared females were fed one of five species of natural or factitious prey: beet armyworm, *Spodoptera exigua* (Hübner); fall armyworm, *Spodoptera frugiperda* (J.E. Smith); cabbage looper, *Trichoplusia ni* (Hübner); wax moth, *Galleria mellonella* (L.); or yellow mealworm, *Tenebrio molitor* (L.). Fresh weights and contents of lipid, protein, and yolk protein were compared over periods of 7, 15, and 22 d. Fresh weights and protein showed no significant differences by trial length or by prey species. Total lipid content was the most significant parameter in relation to time and species of prey, ranging from 5.3 to 15.5% of mean fresh weight. Female *P. maculiventris* varied significantly in total lipid content by prey species at 15 and 22 d, and by week only when fed fall armyworm. Highest lipid contents were observed in females fed yellow mealworm, and lowest lipid contents were observed in females fed cabbage looper and beet armyworm. Yolk protein content did not correlate with cumulative oviposition, but it did vary with time in those females fed on the beet armyworm or the wax moth. Lipid content in female predators may vary inversely with reproductive potential or egg load and offers a quantitative measure of food quality.

**KEY WORDS** predation, food quality, reproduction, ELISA, nutrition

A COMMON CONCEPT IN adaptive biology holds that a generalist predator should prefer and seek prey of high nutritional value, thereby maintaining reproductive and other selective advantages. However, prey preferences of predators have been observed to run counter to this concept (Eubanks and Denno 2000, Venzon et al. 2002, Legaspi and Legaspi 2004). In the anthocorid *Orius laevigatus* (Fieber), prey preference correlated best with patch productivity, i.e., the total number of offspring per female per patch that survived until adulthood (Venzon et al. 2002). With *Geocoris punctipes* (Say), prey preference correlated with mobility of the prey (Eubanks and Denno 2000). To determine whether the prey preference of the adult generalist predator *Podisus maculiventris* (Say) coincides with its nutritional interests, Legaspi and Legaspi (2004) examined the reproductive output of females over 1- to 4-wk periods in relation to their consumption of prey over a 24-h period, given a choice of five species of immature Coleoptera and Lepidoptera. They found that starved female *P. maculiventris* consumed beet armyworm, *Spodoptera exigua* (Hübner), at the highest rate of any prey, but the cumulative number of eggs produced did not clearly coincide with numbers or biomass consumed.

Implicit in these analyses is that the nutritional value, or food quality, of prey is critical to the survival and reproduction of the predator. However, both definition and determination of the food quality of prey remain elusive. Food quality has been defined for herbivores in terms of nitrogen content (Di Giulio and Edwards 2003) or lack of allelochemicals (Stamp et al. 1991, Slansky and Wheeler 1992, Jansen and Stamp 1997). For predators, development of immatures (Oelbermann and Scheu 2002), utilization efficiency and consumption capacity (Toft 2005), or production of eggs in response to feeding (Evans et al. 1999, Marcussen et al. 1999, Evans 2000) have been used to define food quality. Evans et al. (1999) noted earlier distinctions between "essential" and "alternative" prey, where essential prey can support the growth and development of immatures and reproductive development of adults, whereas alternative prey only provide for maintenance of a life stage (Hodek 1962, Hodek and Honek 1996). They also noted that the distinction is based on single-item diets and is thus idealized, and they demonstrated that a diet of alternative prey supplemented with small amounts of essential prey or carbohydrate provided better nutrition for female reproduction than a diet of alternative prey alone.

The variable quality of food in relation to egg production also may be seen in studies where a minimal artificial diet for a predator is supplemented with defined components. In *Orius insidiosus* (Say), semipurified proteins from prey were shown to enhance egg production at concentrations 8- to 80-fold lower than proteins from several noninsect sources (Ferkovich and Shapiro 2004). We suggest that a generalist feeder such as *O. insidiosus* can adapt to a suboptimal food (or alternative prey), but that its full reproductive potential can be reached only by meeting specific nutritional requirements with essential prey or selected biochemical components thereof. The food quality of a species of prey can therefore be evaluated by measuring reproductive responses of the predator to that prey and by characterizing specific biochemical components of essential prey in light of those responses.

We have selected female reproductive development as a prey-dependent process that is stringent in its nutritional requirements, especially relative to the development of immature stages. Two primary goals of the current study may be advanced by examining the effects of various prey on adult reproduction: 1) to discover sensitive indicators of the food quality of prey and 2) to advance our ability to analytically determine food quality. To survey some basic biochemical parameters that may predict reproductive performance, we have compared the compositions of *P. maculiventris* females fed on a range of prey over a 3-wk period. This work extends a study by Legaspi and Legaspi (2004) using insects from that study.

## Materials and Methods

**Insects.** *P. maculiventris* from previously described experiments (Legaspi and Legaspi 2004) were reared at 26°C and a photoperiod of 14:10 (L:D) h as nymphs on yellow mealworm, *Tenebrio molitor* (L.), larvae. Within 2 to 3 d of molt, adults were starved for 24 h and then fed one individual third or fourth instar per day of one of five prey species: beet armyworm; fall armyworm, *Spodoptera frugiperda* (J.E. Smith); wax moth, *Galleria mellonella* (L.); cabbage looper, *Trichoplusia ni* (Hübner); and yellow mealworm *Tenebrio molitor*. After feeding for 7, 15, or 22 d, female *P. maculiventris* were collected, live weights were taken, and they were stored at −80°C pending biochemical analyses.

**Extractions.** Each insect was homogenized on ice for 1 min with a Polytron homogenizer (Brinkmann Instruments, Westbury, NY) in 19.9 ml of phosphate-buffered saline containing 100 μl of a protease inhibitor cocktail (Sigma, St. Louis, MO). Using the Bligh-Dyer method (Bligh and Dyer 1959), lipids were extracted by vigorously mixing 1.0 ml (equivalent to 0.05 insect) of the homogenate with 3.75 ml of chloroform/methanol (1:2) and 20 mg of $Na_2SO_4$. Chloroform (1.25 ml) was added with more mixing, and the lipid (chloroform) phase was removed. To the methanolic phase, 1.88 ml of chloroform was added, and the extraction was repeated; lipid phases were combined. The lipid extract was brought to 7.0 ml, and 1.0 ml (0.00714 insect-equivalents) was removed and dried under $N_2$ for transmethylation and fatty acid analysis. The remaining 6.0 ml of lipid extract (0.0429 insect-equivalents) were dried in a SpeedVac for determination of total lipid.

**Biochemical Analyses.** Total lipid was determined by the vanillin method (Vanhandel 1985; Vanhandel and Day 1988; Warburg and Yuval 1996, 1997; Yuval et al. 1998), by using a triolein as a quantitative standard in a 50–2,000-μg serial dilution. To standards or the residue from 6.0 ml of extract, 0.5 ml of $H_2SO_4$ was added, lipids were hydrolyzed at 90°C, and 10 μl of hydrolyzed sample was added to 190 μl of vanillin reagent. Color was read at 530 nm in a plate reader and quantities were interpolated from a standard curve using KCjunior software (Bio-Tek Instruments, Winooski, VT).

Total soluble trichloroacetic acid (TCA)-precipitable protein was determined using the Pierce Chemical (Rockford, IL) bicinchoninic acid protein assay (Smith et al. 1985). Particulates were removed from aqueous homogenates by centrifugation for 1 min at 21,000 × *g*, and 200 μl of the supernatant was diluted in 300 μl of $H_2O$ and 100 μl of sodium deoxycholate. Protein was precipitated by adding 100 μl of 72% TCA and centrifuging 10 min at 21,000 × *g*. Samples were redissolved in 50 μl of 5% sodium dodecyl sulfate and quantified from a standard curve by using bovine serum albumin standards (precipitated as described above). Color was read by a plate reader (Bio-Tek Instruments) at 562 nm, and results were interpolated from a standard curve.

Yolk protein contents were determined from the centrifuged aqueous homogenates by using a direct antigen enzyme-linked immunosorbent assay (ELISA), modified from the indirect antigen YP-ELISA for *P. maculiventris* (Shapiro and Ferkovich 2002). Monoclonal antibody 4C9-2D5 (MAb), which reacts against the *P. maculiventris* 171,000 molecular weight yolk polypeptide (Shapiro et al. 2000), was conjugated with horseradish peroxidase (HRP) by using the Versalinx kit (Calbiochem/EMD Biosciences, San Diego, CA). Antibody was concentrated to 3.6 mg/ml in 50 mM sodium bicarbonate buffer, pH 8.5, by using a 30-kDa molecular weight cut-off spin column, activated with phenyldiboronic acid-NHS amine-modifying reagent, and then with salicylhydroxamic acid-modified HRP. A 3:1 mass ratio of HRP to MAb was used. The YP-ELISA (Shapiro and Ferkovich 2002) was modified by substituting the original 4C9-2D5 primary antibody with the HRP-conjugated 4C9-2D5 (21 μg/ml), eliminating the need for a secondary rabbit anti-mouse antibody for detection.

**Statistics.** Data were statistically analyzed using Statistica software version 7.0 (StatSoft, Tulsa, OK). Significant ($P < 0.05$) one-way analysis of variance (ANOVA) was followed post hoc by the Tukey's honestly significant difference (HSD) test for group means comparison.

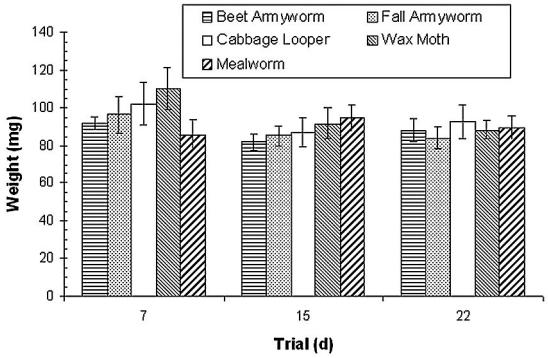


**Fig. 1.** Live weights of *P. maculiventris* fed five species of prey, at the conclusion of 7-, 15, and 22-d trials.

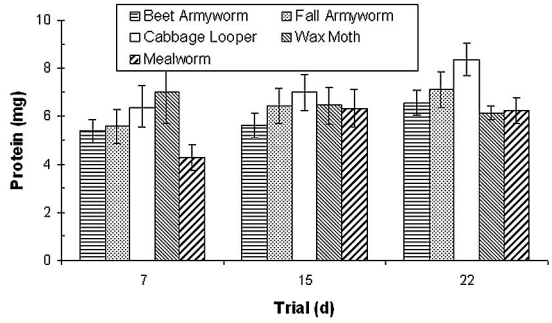


**Fig. 2.** Soluble, TCA-precipitated protein content of *P. maculiventris* fed five species of prey, at the conclusion of 7-, 15, and 22-d trials.

## Results

**Weight and Total Protein Content.** For all trials and all prey, fresh body weight (Fig. 1) and total soluble protein (Fig. 2) did not vary significantly by week or by species of prey (Table 1, all trials), although the general trend was toward a decrease in weight and increase in protein content with increased trial period. When the highest (cabbage looper, 7.04 ± 0.05 mg per insect) and lowest (mealworm, 5.33 ± 0.40 mg per insect) total soluble protein contents were considered across all trials, differences were highly significant ($F = 7.18$, df = 1, $P = 0.01$). The protein content of females feeding on specific prey made up from 4.7 to 9.1% of mean body weight (all trials) in mealworm- (7-d trial) and cabbage looper-fed bugs (22-d), respectively. Only mealworm-fed bugs showed significant change among trial periods ($F = 4.1$, df = 2, $P = 0.035$), decreasing slightly with time from 6.97 to 6.12 mg per bug.

Body weights ranged from 80 to 110 mg. The highest mean body weights were achieved by female *P. maculiventris* that consumed wax moth, mealworm, and cabbage looper larvae (7-, 15-, and 22-d trials, respectively) and lowest weights by those feeding on mealworm, beet armyworm, and fall armyworm (7-, 15-, and 22-d trials, respectively).

**Lipid Content.** Lipid content (Fig. 3) varied significantly with the species of prey consumed ($F = 8.00$, df = 4, $P = 0.00001$; Table 1), notably among species of prey in the 7-d ($F = 2.78$, df = 4, $P = 0.038$) and 15-d ($F = 7.53$; df = 4, $P = 0.0002$) trials. In mealworm-fed females, lipid content reached high values of 14.2 (15-d trial) and 13.99 mg per female (22-d), constituting 15.5% of total mean weight. This is almost threefold greater than the lowest lipid contents, seen in fall armyworm-fed (4.5 mg per female, or 5.3% of total mean weight; 22-d trial) and cabbage looper-fed females (4.8 mg per female, 15- and 22-d trials). There was no consistent pattern of change in lipid content

**Table 1. Effects of prey diet and trial period on live weight, total protein and lipid, and yolk protein in *P. maculiventris* females**

| Time trial | Prey species | | | | | | | | | | | | Statistics | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | BAW | *n* | FAW | *n* | CL | *n* | WAX | *n* | MW | *n* | All Prey | *n* | *F* | P | df |
| 7-d trial | | | | | | | | | | | | | | | |
| Wt | 92.0 ± 3.5 | 10 | 96.2 ± 10.0 | 10 | 102.3 ± 11.5 | 10 | 110.5 ± 11.1 | 9 | 85.2 ± 8.5 | 10 | 96.98 ± 4.17 | 49 | 1.06 | 0.39 | 4 |
| Protein | 5.39 ± 0.46 | 10 | 5.58 ± 0.73 | 10 | 6.39 ± 0.85 | 10 | 6.97 ± 1.24 | 9 | 4.30 ± 0.52 | 10 | 5.70 ± 0.36 | 49 | 1.65 | 0.18 | 4 |
| Lipid | 11.37 ± 0.84 | 10 | 6.67 ± 0.96 | 10 | 9.24 ± 1.30 | 10 | 11.33 ± 1.50 | 9 | 10.61 ± 1.29 | 10 | 9.81 ± 0.57 | 49 | 2.78* | 0.04 | 4 |
| Yolk protein | 217.1 ± 31.8 | 10 | 179.4 ± 39.1 | 10 | 204.3 ± 21.2 | 10 | 284.1 ± 55.8 | 9 | 127.8 ± 34.0 | 10 | 200.9 ± 17.5 | 49 | 2.26 | 0.08 | 4 |
| 15-d trial | | | | | | | | | | | | | | | 4 |
| Wt | 81.73 ± 2.78 | 9 | 85.28 ± 5.36 | 9 | 87.17 ± 7.86 | 6 | 91.64 ± 8.19 | 7 | 94.56 ± 7.01 | 5 | 87.23 ± 2.78 | 36 | 0.61 | 0.66 | 4 |
| Protein | 5.62 ± 0.48 | 9 | 6.43 ± 0.74 | 9 | 7.01 ± 0.75 | 6 | 6.44 ± 0.77 | 8 | 6.32 ± 0.80 | 5 | 6.32 ± 0.31 | 37 | 0.51 | 0.73 | 4 |
| Lipid | 9.20 ± 0.69 | 9 | 8.61 ± 1.05 | 9 | 4.84 ± 1.12 | 6 | 7.78 ± 1.01 | 8 | 14.22 ± 1.70 | 5 | 8.72 ± 0.62 | 37 | 7.53* | <0.001 | 4 |
| Yolk protein | 152.3 ± 31.1 | 9 | 217.6 ± 63.8 | 9 | 180.7 ± 32.8 | 8 | 121.9 ± 32.6 | 9 | 203.8 ± 36.3 | 6 | 173.1 ± 19.0 | 41 | 0.86 | 0.50 | 4 |
| 22-d trial | | | | | | | | | | | | | | | 4 |
| Wt | 88.1 ± 6.0 | 9 | 83.8 ± 5.9 | 6 | 92.7 ± 8.8 | 5 | 88.3 ± 4.9 | 8 | 89.4 ± 6.5 | 7 | 88.3 ± 2.7 | 35 | 0.21 | 0.93 | 4 |
| Protein | 6.56 ± 0.50 | 9 | 7.11 ± 0.72 | 6 | 8.36 ± 0.66 | 5 | 6.12 ± 0.27 | 8 | 6.23 ± 0.51 | 6 | 6.76 ± 0.26 | 34 | 2.50 | 0.06 | 4 |
| Lipid | 10.66 ± 2.04 | 9 | 4.54 ± 0.48 | 6 | 4.82 ± 0.70 | 4 | 7.49 ± 1.01 | 8 | 13.95 ± 2.52 | 6 | 8.67 ± 0.94 | 33 | 4.70* | <0.005 | 4 |
| Yolk protein | 126.2 ± 18.0 | 9 | 167.8 ± 42.3 | 6 | 132.6 ± 34.0 | 4 | 96.9 ± 16.1 | 8 | 106.1 ± 19.3 | 7 | 123.2 ± 11.2 | 34 | 1.41 | 0.25 | 4 |
| All trials | | | | | | | | | | | | | | | |
| Wt | 87.48 ± 2.71 | 28 | 89.30 ± 4.63 | 25 | 97.63 ± 5.29 | 21 | 97.63 ± 5.29 | 24 | 88.63 ± 4.53 | 22 | 91.54 ± 2.08 | 120 | 0.98 | 0.42 | 4 |
| Protein | 5.84 ± 0.28 | 28 | 6.25 ± 0.43 | 25 | 6.53 ± 0.50 | 21 | 6.53 ± 0.50 | 25 | 5.33 ± 0.40 | 22 | 6.19 ± 0.19 | 120 | 2.15 | 0.08 | 4 |
| Lipid | 10.44 ± 0.74 | 28 | 6.86 ± 0.62 | 25 | 8.96 ± 0.77 | 20 | 8.96 ± 0.77 | 25 | 12.42 ± 1.05 | 25 | 9.16 ± 0.40 | 119 | 8.01* | 0.00 | 4 |
| Yolk protein | 167.1 ± 17.3 | 28 | 190.4 ± 28.7 | 25 | 170.4 ± 27.6 | 22 | 170.4 ± 27.6 | 26 | 141.1 ± 19.6 | 23 | 162.21 ± 9.60 | 124 | 0.34 | 0.85 | 4 |

Weighted means ± SE. Statistics exclude the "All prey" column.
BAW, beet armyworm; CL, cabbage looper; FAW, fall armyworm; MW, yellow mealworm; and WAX, wax moth.

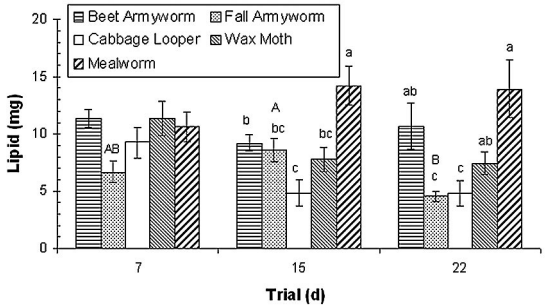


**Fig. 3.** Lipid content of *P. maculiventris* fed five species of prey, at the conclusion of 7-, 15, and 22-d trials. Means significantly different within the same trial are denoted by different lowercase letters; means significantly different between trials are denoted by different uppercase letters.

with trial period, and only in fall armyworm-fed females did lipid vary significantly with trial period ($F = 3.92$, df = 2, $P = 0.035$). Lipid content inversely correlated with prey species that yielded the lowest or highest eggs per clutch and egg clutches per female.

**Yolk Protein Content.** Yolk protein content varied significantly with trial period ($F = 5.06$, df = 2, $P = 0.008$), but not with prey. The general trend was toward a decrease in yolk protein with trial period, especially between the 15- and 22-d trials (Fig. 4). When yolk protein contents were compared with oviposition, calculated cumulatively to the conclusion of each of the three trial periods (Legaspi and Legaspi 2004), regression analysis showed no significant correlation.

## Discussion

All of the prey (beet armyworm, fall armyworm, and cabbage looper) or factitious prey (wax moth and mealworm) used in these studies could be classed as essential prey for *P. maculiventris*, judging by observed oviposition rates (Legaspi and Legaspi 2004). Of the biochemical contents of *P. maculiventris* among females fed those species, lipid content varied the most with different diets. Females fed on *G. mellonella* had

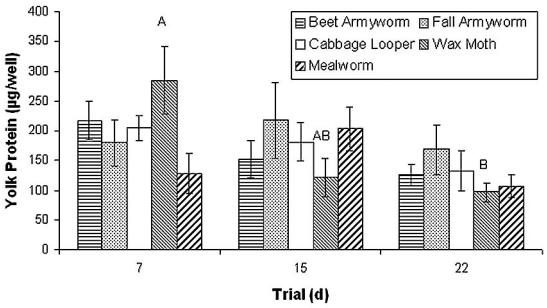


**Fig. 4.** Yolk protein content of *P. maculiventris* fed five species of prey, at the conclusion of 7-, 15, and 22-d trials. Means significantly different between trials are denoted by different uppercase letters.

been previously shown to attain full ovarian development, measured as ovariole length, at 9 d or later after eclosion (Shapiro et al. 2000). In the current study, at the conclusion of the 15- and 22-d feeding trials, minimal lipid content was found in females fed a diet of cabbage loopers and maximal lipid content in those fed mealworms. Cumulative oviposition of these females was inversely related to lipid content: maximal oviposition by those fed cabbage loopers and minimal oviposition by those fed mealworms, for either 15 or 22 d (Legaspi and Legaspi 2004). Cabbage loopers provided the highest and mealworms the lowest food quality in that study with respect to eggs per clutch and number of clutches in the 22-d trial. When availability of food to *P. maculiventris* females was limited to determine the effects of food deprivation on egg production, Legaspi and O'Neil (1994) found that increased intervals between feedings resulted in lower oviposition rates and egg loads, and higher lipid contents. They noted a trade-off between reproduction and longevity in unmated female *P. maculiventris* and found that increased intervals between feedings resulted in lower oviposition rates and egg loads, and higher lipid contents. A similar relationship was seen in three species of predatory bugs in the genus *Anthocorus*, which do not mature eggs unless mated. In all three species, unmated females contained more somatic lipid than mated females. This relationship between metabolic stores and ovarian development highlights the metabolic trade-off between reproduction and other functions (Horton et al. 2005), and ultimately the overall plasticity and adaptability of ovarian development to nutrition (Wheeler 1996) and other environmental conditions (Papaj 2000).

In contrast to effects on lipid content, the species of prey had no effect on weight or total protein content of female *P. maculiventris.* Yolk protein content was expected to show the differential effects of prey but it did not, perhaps because of variability. Some decrease in yolk protein was seen over time, notably in females fed wax moth larvae. Legaspi and Legaspi (2004) correlated differences in egg maturity with increased length of trial and concomitant increase in the age of insects, showing decreased numbers of mature eggs and increases in immature eggs, corresponding to our decrease in yolk protein. As opposed to cumulative oviposition data, which comprise integrated daily oviposition rates, analyses by dissection (Legaspi and Legaspi 2004) or by yolk protein ELISA (Shapiro and Ferkovich 2002) yield a static measure of reproductive capacity at the time of sample collection, equivalent or comparable with determinations of egg load (Minkenberg et al. 1992, Legaspi et al. 1996, De Clercq and Degheele 1997, Ellers et al. 2000, Papaj 2000, Legaspi and Legaspi 2005). These static measures have the advantage of a one-time rapid measurement and can yield data from field as well as laboratory specimens, whereas oviposition data must be collected from captive laboratory or field-caged specimens.

The success of *P. maculiventris* as a generalist challenged our goal of discovering sensitive indicators of response to the food quality of prey with regard to

reproduction in the predator, because most biochemical indicators and reproductive measures showed little or no difference among the wide range of five species of natural and factitious prey from two orders. Other choices of prey species might have represented more disparity in food quality, as with the predators *Anthocoris nemorum* and *A. nemoralis* fed *Aphis fabae* Scopoli as low-quality prey and other aphid species as high-quality prey (Meyling et al. 2003). Complicating factors such as prior experience with other prey species (Henaut et al. 2000), consumption of mixtures of alternative prey (Evans 2000), or consumption of plants by omnivorous predators (Coll 1996, Coll et al. 1997, Agrawal and Klein 2000) may all affect the food quality of prey for a predator.

We propose that the reciprocal relationship between lipid content of the predator and its mature egg load or oviposition rate may offer a useful correlate and a means to measure food quality through nutritional effects on adult female predators. Ellers (1996) came to a similar conclusion in studying a hymenopterous parasitoid, *Asobara tabida* (Nees). The number of eggs in ovarioles was negatively correlated with fat content of the parasitoid, and fat content was positively correlated with longevity and negatively with age. Measurement of fat content was proposed as an efficient means to study trade-offs between reproduction and survival. In other species, changes in lipid content may signal shifts in other behaviors, e.g., from reproduction toward diapause or dispersal. For predators, these shifts may be triggered by changing quality or quantity of prey with changes in environmental conditions.

In contrast to lipid content, the species of prey that was consumed affected neither weights nor protein content of female *P. maculiventris*, corresponding to previous observations in which weights of *P. maculiventris* did not differ when fed throughout their life cycle on wax moth or mealworm larvae, whereas development and oviposition rates were greater when fed the former (De Clercq et al. 1998). That work supports the view that vitellogenesis in predators is a more nutritionally stringent process than nymphal development. Therefore, discovery of dietary components that fully satisfy requirements for ovarian development are likely to satisfy nymphal needs as well.

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